
Taxonomic Evaluation and New Combinations in the *Lupinus gibertianus*–*L. linearis* Complex (Fabaceae)

Ana María Planchuelo and Elsa Fuentes

ACOR, Facultad de Ciencias Agropecuarias, Universidad Nacional Córdoba, Casilla de Correo 509, 5000 Córdoba, Argentina

ABSTRACT. The *Lupinus gibertianus*–*L. linearis* complex was evaluated using nomenclature reviews, studies of all type material, and multivariate analysis. The results support the recognition of *L. linearis* Desrousseaux and three varieties of *L. gibertianus* C. P. Smith. The new combinations *L. gibertianus* var. *reineckianus* Planchuelo & E. Fuentes and *L. gibertianus* var. *berroanus* Planchuelo & E. Fuentes are made. Taxonomic keys, descriptions, illustrations, and synonymy are included, and representative specimens are listed.

RESUMEN. Se evalúa taxonómicamente el complejo *Lupinus gibertianus*–*L. linearis* realizando una revisión nomenclatural, un estudio de materiales tipos y una evaluación de caracteres morfológicos mediante técnicas de análisis multivariado. Los resultados soportan el reconocimiento de *L. linearis* Desrousseaux y tres variedades de *L. gibertianus* C. P. Smith. Se dan a conocer las nuevas combinaciones *L. gibertianus* var. *reineckianus* Planchuelo & E. Fuentes y *L. gibertianus* var. *berroanus* Planchuelo & E. Fuentes. El trabajo se completa con una clave identificatoria, descripciones, sinonimias, ilustraciones y lista de especímenes representativos de los taxa tratados.

Key words: Fabaceae, *Lupinus*, New World.

Lupinus L. is primarily a New World genus with approximately 600 species (Planchuelo, 1982), which show a range of variation from annual to perennial and from acaulescent or small prostrate to tree-like shrubs up to 4–4.5 m tall (Dunn, 1984). The species treated in this paper, *L. gibertianus* C. P. Smith and *L. linearis* Desrousseaux, grow in eastern South America (Atlantic sub-Region; Planchuelo-Ravelo, 1984; Planchuelo, 1994a), mainly in northeastern Argentina, with few representatives in eastern Brazil, Paraguay, and Uruguay. Both species are clearly different from the simple-leaved lupines (Planchuelo & Dunn, 1984, 1989) and are distinguished from other compound-leaved lupines growing in the same area by the annual habit, indument without spreading hairs, and free tip of the stipules not foliaceous (Planchuelo, 1996b).

Lupinus gibertianus is a polymorphic species, and because of its enormous morphological complexity several taxa have been described at specific and varietal levels. Dunn and Planchuelo (1981) clarified the nomenclatural ambiguity of the taxa involved by accepting *L. gibertianus* as the correct name rather than *L. heptaphyllus* (Vellozo) Hassler or *L. hilarianus* Benthham, pending the evaluation of morphological characters. Dunn (1984) pointed out that this species is essentially self-pollinated, with numerous genetic differences by geographic area. *Lupinus linearis*, native to the same areas as *L. gibertianus*, is a closely related species differing mainly by its branching structure and leaflet shape. Both species were treated by Planchuelo-Ravelo (1991) and Planchuelo (1996a) as a complex with great morphological variation and sympatric distribution.

Chemotaxonomic evaluation of alkaloid profiles (Planchuelo-Ravelo et al., 1993; Planchuelo, 1994b), seed oil components (Fuentes & Planchuelo, 1997), alkanes of leaf waxes (Merino et al., 1999), and flavonoids (Merino et al., 2000) shows that *L. linearis* and *L. gibertianus* have phytochemical patterns very different from other lupines growing in South America. The major alkaloid and alkane components of *L. gibertianus* and *L. linearis* are similar, although differences in qualitative and quantitative patterns were found between the two species and the vouchers that represent different populations of *L. gibertianus* (Planchuelo, 1994b; Merino et al., 1999).

In an effort to define the taxa of this complex, numerous herbarium specimens as well as type materials, when available, were evaluated. Vegetative and floral characters were analyzed by numerical taxonomy techniques.

MATERIALS AND METHODS

This study is based chiefly on herbarium specimens from the following herbaria: ACOR, B, BA, BAA, BAB, BAF, CORD, CTES, DS, F, G, K, LIL, LP, LSR, MO, P, RNG, SI, UC, UMO, and US. Information on habitat and ecology of the species was

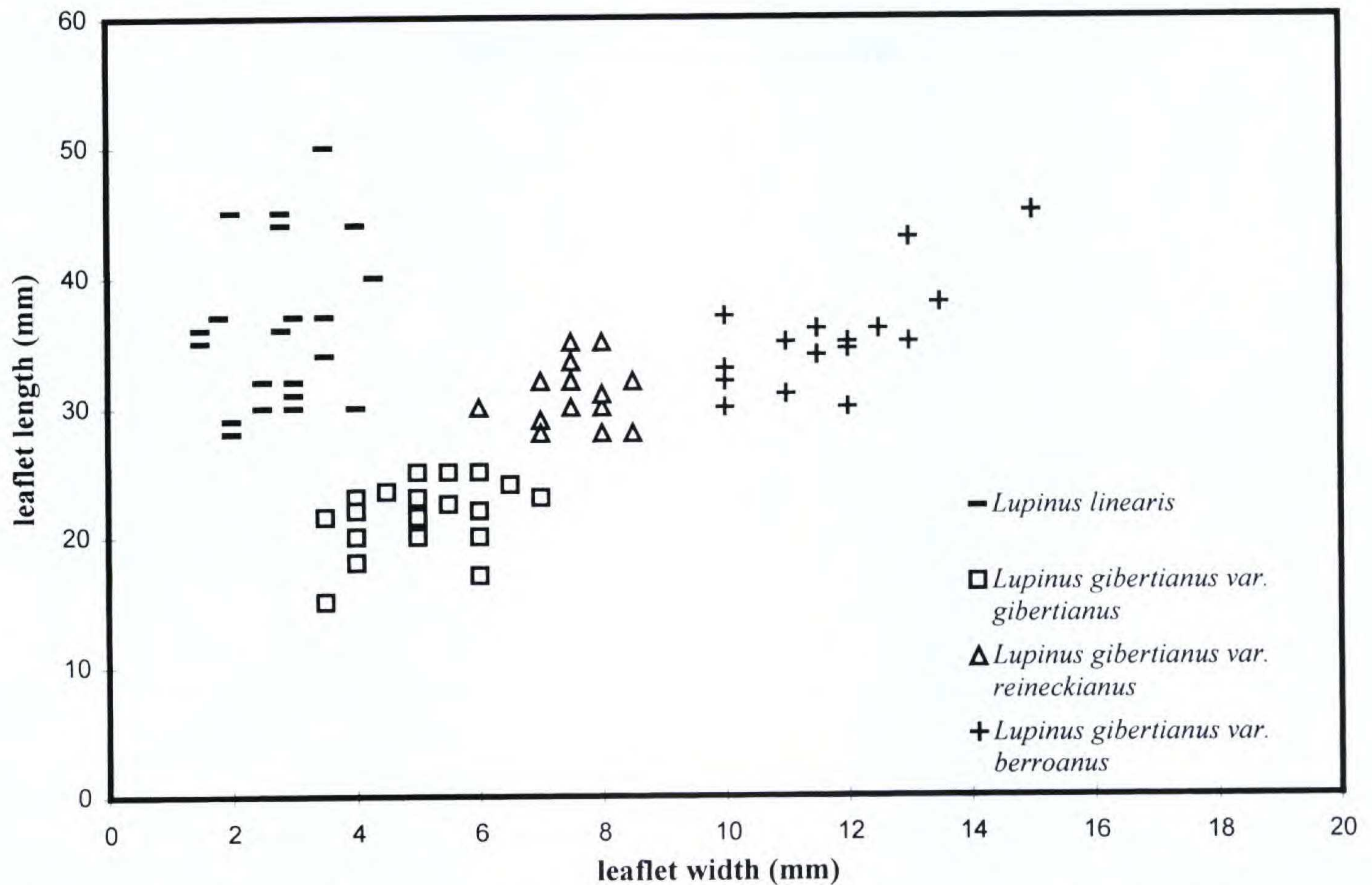


Figure 1. Scatter diagram showing the leaflet length and maximum width relationship of the 90 voucher specimens that are marked by an asterisk in the specimens examined lists (due to overlap, only 70 are distinguished in the diagram).

taken from herbarium specimen labels and from personal observations of the plants in the field.

Representative specimens of *L. linearis* and *L. gibertianus*, as well as type material of names treated in Dunn and Planchuelo (1981), were included in the data matrices in order to establish the relationship between the taxa. Vegetative and floral structures were studied, and measurements were taken from fully mature organs according to Planchuelo (1978). Each character was considered an independent variable, and the data recorded was the mode of that character for each specimen. To evaluate the differences in leaflet sizes and shapes, a scatter diagram was constructed with 90 data entries using leaflet length and leaflet width as parameters. Specimens cited herein and included in this analysis are marked by asterisks (*). The data matrix is available upon request from the author. A leaflet shape coefficient (LSC), based on the relationship between the width at midpoint and the maximum width of the leaflets, was developed to characterize the differences between linear and ob-lanceolate leaflet shapes.

$$\text{LSC} = W_{\text{mid}}/W_{\text{max}}$$

Where:

LSC = Leaflet Shape Coefficient

W_{mid} = leaflet width at leaflet mid-point

W_{max} = maximum leaflet width

Numerical Taxonomy and the Multivariate Analysis System (Rohlf, 1992) were applied in order to evaluate a wide range of vegetative and floral characters. Fourteen morphometric parameters relative to size and shape were evaluated for the 50 Operational Taxonomic Units (OTUs): petiole (length), leaflets (length, maximum width, half-length width, LSC), stipules (free portion length, free portion width), calyx (lower lip length, upper lip lobe width), and corolla (banner length, banner maximum width, wing length, wing width, keel width). The voucher specimens are identified by their OTU's number (in brackets) in the list of representative specimens. The data matrix was analyzed using distance coefficients and the unweighted pair grouping method of arithmetic average (UPGMA) (Crisci & López Armengol, 1983).

RESULTS

The scatter diagram (Fig. 1) shows four major groups, one corresponding to *L. linearis* and the other three we recognize as varieties of *L. gibertianus*. Due to overlap, only 70 of the 90 data entries are distinguished in the diagram.

The phenetic cluster analysis (Fig. 2) shows two

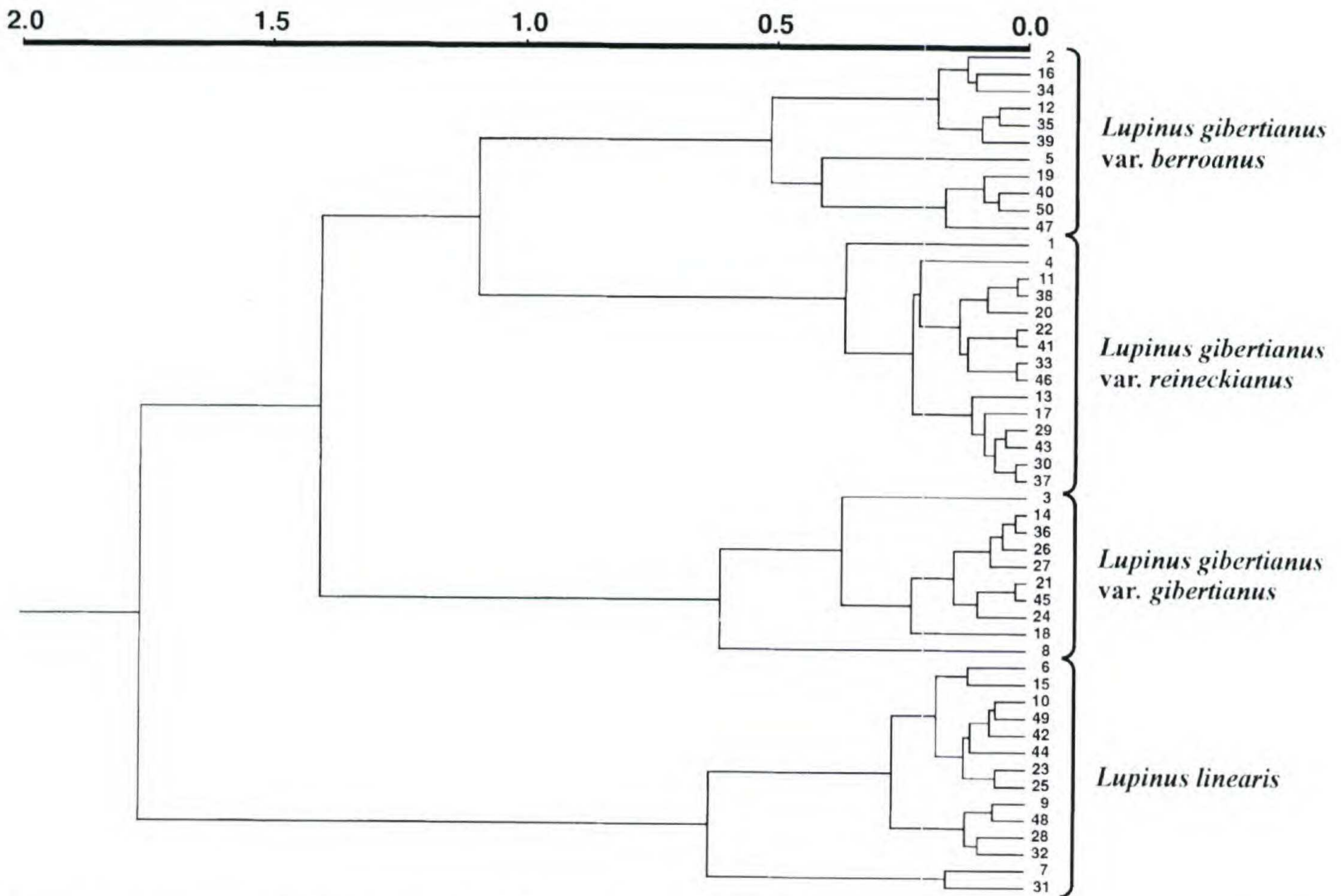


Figure 2. Phenogram of 50 OTUs based on 14 vegetative and floral characters analyzed by a distance coefficient and unweighted pair grouping method of arithmetic average (UPGMA).

main groups. One cluster comprises all representative OTUs of *L. linearis*, and the other cluster has two secondary branches. One of them includes all specimens of *L. gibertianus* var. *gibertianus*, and the other is divided into two tertiary branches that represent *L. gibertianus* var. *berroanus* and *L. gibertianus* var. *reineckianus*.

These results show that *L. linearis* is clearly separate from *L. gibertianus* and that subdivisions within *L. gibertianus* can be recognized. The characters enumerated in the following key allowed the identification of the species and the varieties proposed.

KEY TO THE SPECIES AND VARIETIES OF THE *LUPINUS GIBERTIANUS*-*L. LINEARIS* COMPLEX

- 1a. Juvenile plants with a basal rosette of leaves, adult plants usually branching below; leaflets (28-)30-50 × 1.5-3.5(-4.5) mm, linear or occasionally narrowly lanceolate-attenuate; Leaflet Shape Coefficient (LSC) = 1; racemes terminal not appearing lateral 1. *L. linearis*
- 1b. Juvenile plants without a basal rosette of leaves, adult plants usually branching above; leaflets (15-)20-40(-45) × (3-)4-12(-15) mm, narrowly to broadly oblanceolate, not linear or lanceolate-attenuate, when less than 4.5 mm wide no longer than 25 mm; LSC = 0.60-0.90; racemes terminal but sometimes appearing lateral when the top

- lateral bud grows rapidly and vertically 2. *L. gibertianus*
- 2a. Leaflets 15-25 × (3.5-)4-6(-7) mm; free portion of the stipules 1.5-2.5 × 0.5-1 mm; standard petal 7-8 × 4.5-6 mm 2a. *L. gibertianus* var. *gibertianus*
- 2b. Leaflets 28-40(-45) × (6-)7-13(-15) mm; free portion of the stipules 3-4(-5) × 1-1.5 mm; standard petal 8-11 × 7-10 mm 2b. *L. gibertianus* var. *reineckianus*
- 3a. Leaflets (6-)7-8.5(-9) mm wide, oblanceolate, apex acute; LSC = 0.80-0.90; standard petal 10-11 × 9-10 mm 2c. *L. gibertianus* var. *berroanus*

1. *Lupinus linearis* Desrousseaux, Lam. Encyclop. 3: 625. 1791. TYPE: Uruguay. Montevideo, Oct. 1925, *Commerson s.n.*, *Herb. de Jussieu* (holotype, P-JU; ACOR photo, F photo).

Lupinus pseudolinearis (Hassler) C. P. Smith, Spec. Lupinorum 21: 332. 1943. Syn. nov. Basionym: *Lupinus heptaphyllus* f. *pseudolinearis* Hassler, Repert. Spec. Nov. Regni Veg. 16: 158. 1919. *Lupinus hilarianus* var. *pseudolinearis* (Hassler) C. P. Smith, Spec. Lupinorum 14: 212. 1940. TYPE: Argentina. Misiones: Posadas, 2 Oct. 1911, *Muniez 6* (lectotype, selected



Figure 3. *Lupinus linearis* Desrousseaux. —A. Habit. —B. Leaf, adaxial side. (Drawn from Planchuelo 651, ACOR.)

here, G—plant designated as B; isoelectotype, BAF—plant designated as A only).

Plants annual, 7–40 cm tall. Juvenile plants with a basal rosette of leaves, adult plants branching below. Stems 2–4 mm diam., slender, somewhat angular from the midveins of the petioles, hollow to fistulous, sparsely strigose to glabrous below, hairs more numerous above; internodes 2–3 cm long. Stipule 4–7 mm long, strigose dorsally, the lanceolate-attenuate free tips 2–5 × 0.5–1 mm. Leaves palmate-compound with 7 to 10 leaflets; petioles (2.5–)4.5–7 cm long, with a green rib on both sides ca. 0.5–0.8 mm wide, pubescence as stems; leaflets linear or occasionally narrowly lanceolate-attenuate, (28–)30–50 × 1.5–3.5(–4.5) mm, mostly conduplicate some complanate, glabrous above, ascending-pilose below, tips acute, with an LSC equal to 1. Racemes terminal, 5–9 cm long, with 15 to 35 flowers, scattered. Bracts ovate-lanceolate, 4 × 1.5 mm, caducous, strigose to sericeous dorsally. Bracteoles lanceolate, 1.0–1.5 × 0.3–0.5 mm, attached ca. 0.3 mm below the lips of the lateral sinuses of the calyx. Pedicel strigose, 1–2 mm long at anthesis, 3–4 mm in fruit. Calyx subsericeous outside, glabrous within, the base not gibbous

above, lips 1.5–2.5 mm connate; lower lip lanceolate, 7–9 × 2–3 mm, tridentate, the central tooth 1–2 × 1 mm, the two lateral teeth much smaller; upper lip 5–6 mm long, the lobes 3–4 × 1.5–2 mm. Corolla variable in color changing from intense blue to light blue without purplish tint. Standard petal ovate-obovate, 8–11 × 5–10 mm, clawed, glabrous, appressed 3.5–4 mm, reflexed to 5.5–7 mm, reflexed/appressed: 1.5–1.8, the angle 110–120°. Wings 9–11 mm long including a 2–2.5 mm claw, 4–6 mm wide, lobe above the claw 1.5–2 mm wide. Keel 2.5–4 mm wide in the middle, glabrous, tip blunt, the angle 95–100°. Ovules 8 to 10. Legumes 3–3.8 × 0.5–0.7 cm, sericeous. Seeds 3–4 × 2.6 mm, brown with tan mottling.

Iconography. Figure 3; Planchuelo, 1996a: 111, fig. 1.2.

Phenology. Flowering specimens have been collected from mid September through November, and fruiting specimens from mid November through January.

Habitat. The species grows in open fields with sandy soils and along riverbanks.

Distribution. This species occurs mainly in

northeastern Argentina, Uruguay, Paraguay, and southern Brazil.

Discussion. When C. P. Smith made the new combination *L. hilarianus* var. *pseudolinearis* (Hassler) C. P. Smith, he assigned as type material the collection *Muniez 6* in G and stated “the lefthand specimen alone should stand as the type, since the righthand specimen does not check with the original designation of ‘linearibus,’ having its leaflets much shorter and linear-oblongate, mostly flat.” Later, in 1943 when he recognized the variety as a species, he explained, “This diagnosis is also largely based upon what can be seen in our photograph of the type, taken by us in Geneva in 1930. . .” and also “The right-hand specimen mounted on the same sheet is recorded under *L. hilarianus*, page 331.” Due to the fact that *Muniez 6* includes two plants that represent two different taxa and that the place assigned by Smith for each taxon does not match his descriptions in the actual mounted sheet, we assume that either Smith had a reverse printed photograph or that the collection was remounted on a new sheet with the two plants fixed in different positions. To resolve this situation we designated as lectotype of *L. pseudolinearis* the plant that is mounted on the righthand side of the sheet (assigned by us with the letter B). Furthermore, our interpretation is that *L. pseudolinearis* is a synonym of *L. linearis* because its lectotype is a typical representative plant of the latter taxon and the accompanying plant is clearly identified as *L. gibertianus* var. *gibertianus*.

Representative specimens. *An asterisk indicates a specimen included in this analysis. OTU numbers are in boldface and brackets. ARGENTINA. **Corrientes:** Ituzaingó, Route 34, 13 km SE of Route 12, 11 Oct. 1980, *Schinini & Ahumada 20914* (CTES*) [6]; Mercedes, 4 Nov. 1972, *Sánchez 1001* (BA), 4 Nov. 1973, *Burkart 29908* (SI*) [7]; Paso de Los Libres, 4 Oct. 1993, *Planchuelo 653* (ACOR*) [10]; Ruta 23, 2 km E Río Miriñay, 4 Nov. 1973, *Schinini 7745* (CTES, G, MO, UC); Río Miriñay between Paso de los Libres and Mercedes, 5 Nov. 1973, *Fabris 8608* (LP*) [9]; Parada Pucheta, 6 Nov. 1936, *Parodi 12301* (BAA); San Martín, Yapeyú, 14 Sep. 1979, *Schinini et al. 18426* (CTES); Santo Tomé, 29 Oct. 1970, *Krapovickas & Cristóbal 16374* (CTES*), 3 Oct. 1993, *Planchuelo 652* (ACOR*) [15]; Arroyo Guay Grande, 22 Oct. 1975, *Zardini 1083* (LP). **Misiones:** *Birabén 5415* (LP*), 4 Jan. 1906, *Bonpland s.n.*, herbarium *Hauman Merck 126* (SI, plant mounted on the right side of the sheet*); Parada Seis, 20 Oct., *Burkart 19620* (SI; US); Apóstoles, 22 Sep. 1967, *Krapovickas et al. 15477* (CTES* [23], SI, UC); Aero Club, 3 Oct. 1993, *Planchuelo 651* (ACOR*) [25]; Cainguás, Puerto Rico, 17 Oct. 1947, *Schwindt 443* (LIL plant C); around Posadas, Dec. 1950, *Spegazzini 10810* (BAF*), 2 Oct. 1911, *Muniez 6* (BAF plant designated as A only* [32]; G plant designated as B only); Eldorado, 27 Sep. 1949, *Schwindt 2151* (CTES*; LIL plants A, B, C, D, F, G, H); Puerto

Victoria, 12 Nov. 1949, *Schwindt 2831* (CTES plants mounted in the middle of the herbarium sheet); Iguazú, Puerto Istueta km 14, 20 Sep. 1950, *Montes 9285* (LIL*) [28]; San Ignacio, 11 Oct. 1946, *Medina 58* (LIL plant C); San Pedro, Arroyo Liso, 18 Sep. 1945, *Bertoni 1929* (CTES* [31], LIL); Santa Ana, 30 Nov. 1909, *Rodríguez 58* (SI, plant mounted on the leaf side of isotype of *L. sanctae-anae*), Nov. 1913, *Rodríguez 58* (BA plant designated as A*, no type of *L. sanctae-anae*); San Ignacio, 4 Feb. 1947, *Montes 878* (BA sheet A plant C, sheet B plant A). BRAZIL. **Río Grande do Sul:** Caçapava do Sul, 21 Nov. 1986, *Guerra et al. 2042* (US*) [42]; Porto Alegre, 4 Nov. 1948, *Rambo 37880* (LIL*). PARAGUAY. **Itapúa:** Encarnación, Itacuí, 5 Oct. 1949, *Bertoni 4494* (LIL*) [44]. URUGUAY. Independencia, 24 Oct. 1886, *Safford s.n.* (US 920137*). **Montevideo:** Montevideo, *Commerson s.n.* (G* [48]; P); Cerro, Oct. 1925, *Herter et al. 454A* (B*; G, US); Cerro Casabo, Sep. 1926, *Herter 454* (B, F, G, GH, LIL* [49], MO, NY, UC).

2. *Lupinus gibertianus* C. P. Smith, Spec. Lupinorum 13: 206. 1940. TYPE: Uruguay. Montevideo: 20 July 1866, *Gilbert 467* (holotype, K, ACOR photo; isotypes, MO, UMO, US).

Plants annual, 20–70 cm tall. Juvenile plants without basal rosette of leaves, adult plants branching mainly above. Stems 2–7 mm diam., cylindrical or somewhat angular and \pm hollow or subfistulose in the young branches, strigose; internodes 2–5 cm long. Stipules 4–10 mm long, the free tip lanceolate-caudate, 1.5–4(–5) \times 0.5–1.5 mm. Leaves palmately compound with 5 to 9 leaflets; petioles 1.5–8.2 cm long, pubescence as stems; leaflets (15–) 20–40(–45) \times (3.5–)4–12(–15) mm, when less than 4.5 mm wide no longer than 25 mm, narrowly to broadly oblanceolate, appressed pilose below, glabrous above, with an LSC of 0.60 to 0.90, tips acute to rounded, mucronate. Racemes 4–20 cm long, terminal, but sometimes appearing lateral when the top lateral bud grows rapidly compressing the raceme sideways, with 15 to 45 flowers, scattered. Bracts ovate, 3–4 \times 1–2 mm, caducous, the tip attenuate, sericeous dorsally. Bracteoles lanceolate-ovate to linear-lanceolate, 0.8–2 \times 0.2–0.4 mm, attached 0.5 mm below the lips of the lateral sinuses of the calyx. Pedicel sericeous, 2–4 mm long at anthesis, 3–5 mm in fruit. Calyx sericeous outside, glabrous within, the base sometimes slightly gibbous above, lip connate 1.5–2.0 mm; lower lip (5.5–)6.5–8.0(–10) \times 2–3 mm, normally tridentate, the central tooth (0.2–)1–2 \times 0.3–0.4 mm, the two lateral teeth shorter, sometimes obsolete or reduced to a tuft of hairs at the end of the two lateral veins; upper lip 3–6 mm long, bifid, the lobes 2–4 \times 1–2 mm. Corolla variable in color, changing from purplish to almost white, without blue tint. Standard petal oblong-ovate to oblong-obovate (7–)8–11 \times (4.5–)5–10 mm, clawed, glabrous, appressed 2–4

mm, reflexed 5–8 mm, reflexed/appressed: 1.9–2.5, angle 120–130°. Wings 8–11 mm long including a 1.5–2 mm claw, 4–6 mm wide, lobe above the claw 1–1.5 mm wide. Keel 1.5–4 mm wide in the middle, glabrous, or rarely a few cilia above on the distal half, the angle 90–100°, tip blunt and rounded. Ovules 4 to 8. Legume 3–4 × 0.5–0.7 cm, sericeous. Seeds 3–4 × 2.8 mm, yellowish, covered with very small tan mottling and sparse large tan spots and stripes.

Iconography. Figure 4; Dunn & Planchuelo, 1981: 468, fig. 2; Planchuelo, 1996a: 111, fig. 1.1.

Phenology. Flowering specimens have been collected from early September through December, and fruiting specimens from early October through February.

Habitat. This species shares the same habitat as *L. linearis* and is also found in consolidated dunes (Fuentes & Planchuelo, 2000) and sandy areas with poor vegetation cover.

Distribution. Mainly in eastern Argentina, Uruguay, Paraguay, and southern Brazil.

Discussion. Three varieties of sympatric distribution are identified by the differences in shape and size of the leaflets as major characters, and also by small differences in the free portion of the stipules and the shape and size of the standard petal.

2a. *Lupinus gibertianus* var. *gibertianus*

Lupinus bonplandianus C. P. Smith, Spec. Lupinorum 14: 212. 1940. Syn. nov. TYPE: Argentina. Misiones: June 1821, *Bonpland s.n.* (holotype, P).

Lupinus propedubius C. P. Smith, Spec. Lupinorum 21: 332. 1943. Syn. nov. TYPE: Argentina. Misiones: Grandes malezales de Hibay, 8 Oct. 1886, *Niederlein 1127* (holotype, B lost).

Lupinus sanctae-anae C. P. Smith, Spec. Lupinorum 22: 348. 1944. Syn. nov. TYPE: Argentina. Misiones: Santa Ana, 30 Nov. 1909, *Rodríguez 58* (holotype, DS; ACOR photo, UMO photo; isotypes, LIL, SI—right side of sheet only).

This variety is characterized by short and narrowly oblanceolate leaflets, 15–25 × (3.5–)4–6(–7) mm with an LCS = 0.7–0.9. Free portion of the stipules 1.5–2.5 × 0.5–1 mm. Standard petal 7–8 × 4.5–6 mm.

Iconography. Figure 4B.

Discussion. The holotype of *L. sanctae-anae* (*Rodríguez 58*, DS) and the isotype from LIL are representative of the taxon, but the sheet on which the isotype from SI is mounted includes plants of two different taxa. In this case the plant on the right side of the sheet is the isotype. Another specimen (*Rodríguez 58* from BA) differed from the type by the date of collection, and it is not considered as

type; the two plants of different species mounted on the same sheet were identified according to the citations in this paper.

Representative specimens. *An asterisk indicates a specimen included in this analysis. OTU numbers are in boldface and brackets. ARGENTINA. **Chaco:** Resistencia, Campo Alto, 10 Oct. 1948, *Vega 885* (CTES* [3], LIL). **Corrientes:** Mburucuyá, Ea. Santa Teresa, 4 Sep. 1946, *Pedersen 1* (LP, US); Mercedes, between Solari y Mercedes, 8 Oct. 1971, *Carnevali 2583* (CTES*); Paso de Los Libres, Río Miriñay, 4 Nov. 1973, *Schulz 18646* (CTES*) [8]; San Cosme, Paso de la Patria, 3 Oct. 1945, *Würth 158* (LIL); San Martín, Tres Cerros, 16 Sep. 1979, *Schinini 18582* (CTES*) [14]; Santa Ana, Santa Ana, 14 Nov. 1934, *Parodi 12056* (BAA*); Santo Tomé, Ea. San Francisco, 5 Dec. 1970, *Krapovickas et al. 17195* (BAA*, CTES); Salto Grande, 3 Oct. 1978, *Renvoize 2877* (US*). **Entre Ríos:** Concordia, Río Yuquerí Chico, 13 Oct. 1968, *Cabrera-Sagastegui 19330* (LP*) [18]. **Misiones:** *Montes 14710* (MO), June 1821, *Bonpland s.n.* (P*), 4 Jan. 1906, *Bonpland s.n.*, herbarium *Hauman Merck 126* (SI plants on the middle and left side of the sheet*) [21]; Apóstoles, Escuela Agrotécnica, Oct. 1977, *Cabrera et al. 28566* (SI*) [24]; Cainguás, Puerto Rico, 17 Oct. 1947, *Schwindt 443* (CTES, LIL plants A, B, D, E); Capiovy, 18 Oct. 1948, *Schwindt 771* (CTES*) [26]; Candelaria, Santa Ana, 30 Nov. 1909, *Rodríguez 58* (DS, LIL, SI plant mounted on the right side of the sheet), Nov. 1913, *Rodríguez 58* (BA plant mounted on the right side designated as B*) [27], 17 Sep. 1945, *Montes 1067* (LIL); Mártires, 12 Oct. 1947, *Bertoni 3408* (LIL*); Loreto, 7 Oct. 1946, *Montes 4* (BA); Posadas, 2 Oct. 1911, *Muniez 6* (BAF plant designated as B*; G plant designated as A only), 8 Sep. 1945, *Bertoni 1895* (CTES, LIL); Eldorado, 27 Sep. 1949, *Schwindt 2151* (LIL plant E); Puerto Victoria, 12 Nov. 1949, *Schwindt 2831* (CTES mixed with *L. linearis* in the same sheet, LIL*); San Ignacio, 11 Oct. 1946, *Medina 58* (LIL plants A, B, D, E, F, G, H), 4 Feb. 1947, *Montes 878* (BA sheet A plant B, sheet B plants B, C), 31 Aug. 1949, *Job s.n.* (LP 905476); San Pedro, arroyo Liso, 18 Sep. 1945, *Bertoni 1929* (LIL*). **Santa Fé:** Garray, Cayastá, 3 Nov. 1995, *Planchuelo et al. 817* (ACOR*) [36]; San Jerónimo, Is. Campo Rico, 22 Oct. 1977, *Franceschi 59* (SI). URUGUAY. **Montevideo:** Montevideo, 20 July 1866, *Gibert 467* (K*). **Colonia:** Cerro Carmelo, 6 Dec. 1934, *Cabrera 3198* (LP*) [45]. PARAGUAY. **Curupaty:** Humaitá Neembucú, 9 Nov. 1978, *Rojas 1470* (G*). **Itapúa:** Encarnación, Sep. 1915, *Hassler 1470* (G; SI*).

2c. *Lupinus gibertianus* var. *reineckianus* (C. P. Smith) Planchuelo & E. Fuentes, comb. nov. Basionym: *Lupinus hilarianus* var. *reineckianus* C. P. Smith, Spec. Lupinorum 14: 212. 1940. *Lupinus reineckianus* C. P. Smith, Spec. Lupinorum 30: 484. 1945. TYPE: Brazil. Rio Grande do Sul: 1897, *Reineck & Czermak 93* (holotype, K; ACOR photo, UMO photo; isotype, BA).

Lupinus hassleranus C. P. Smith, Spec. Lupinorum 14: 211. Nov. 1940. Syn. nov. TYPE: Argentina. Misiones: San Ignacio, Oct., *Hassler 444* (holotype, G; UMO photo).

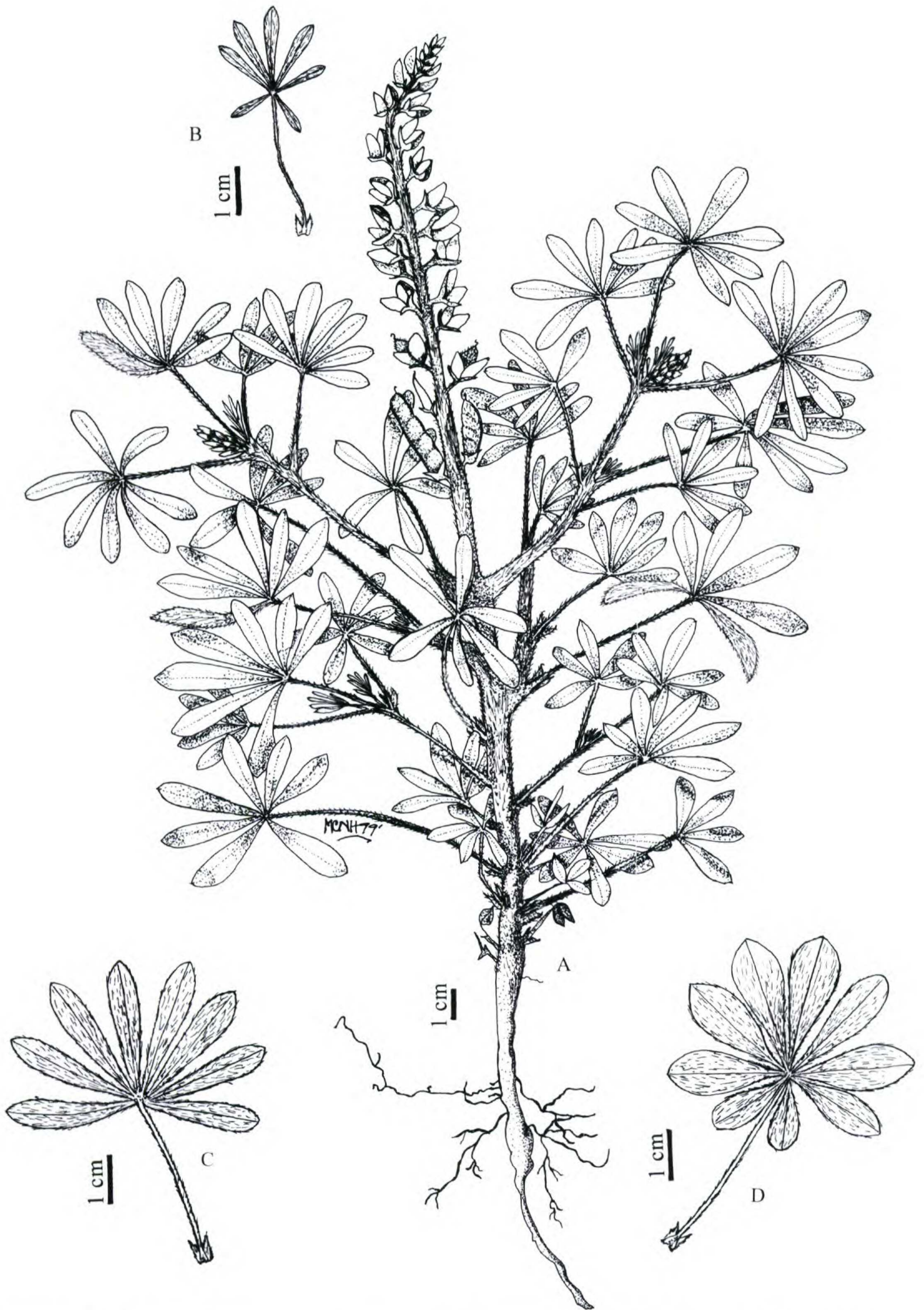


Figure 4. A, C. *Lupinus gibertianus* var. *reineckianus* (C. P. Smith) Planchuelo & E. Fuentes. B. *Lupinus gibertianus* var. *gibertianus*. D. *Lupinus gibertianus* var. *berroanus* (C. P. Smith) Planchuelo & E. Fuentes. —A. Habit. —B. Leaf of variety *gibertianus*, adaxial side (drawn from *Planchuelo et al.* 817, ACOR). —C. Leaf adaxial side (drawn from *Planchuelo* 656, ACOR). —D. Leaf of variety *berroanus*, adaxial side (drawn from *Planchuelo* 609, ACOR).

Lupinus niederleinianus C. P. Smith, Spec. Lupinorum 14: 213. 1940. Syn. nov. TYPE: Argentina. Misiones: Campo Evé, 14 Jan. 1887, *Niederlein 1126* (holotype, B lost; isotype, BA, ACOR photo).

Lupinus rubidus C. P. Smith, Spec. Lupinorum 21: 331. 1943. Syn. nov. TYPE: Argentina. Tucumán: Chicligasta, 14 Oct. 1913, *Monetti 1245* (holotype, DS; ACOR photo, UMO photo; isotypes, GH, LIL).

Lupinus aspersus C. P. Smith, Spec. Lupinorum 22: 345. 1944. Syn. nov. TYPE: Argentina. Santa Fé: Chaco Santafecino, Mocoví, 26 Oct. 1903, *Venturi 92* (holotype, DS; ACOR photo, UMO photo; isotypes, BA, BAA, CORD, LIL, US).

Lupinus palmarum C. P. Smith, Spec. Lupinorum 22: 347. 1944. Syn. nov. TYPE: Argentina. Chaco: Las Palmas, Oct. 1917, *Jørgensen 2139* (holotype, DS; ACOR photo, UMO photo; isotypes, LIL, SI).

This variety is characterized by its oblanceolate leaflets, 28–38 × (6–)7–8.5(–9) mm with an LSC = 0.80–0.90. Free portion of the stipules 3–4(–5) × 1(–1.5) mm. Standard petal 10–11 × 9–10 mm. *Iconography.* Figure 4A, C.

Discussion. *Venturi 92* was cited by C. P. Smith as the holotype of *L. aspersus* (DS); earlier the same author (Spec. Lupinorum 21: 331, 1943) cited the specimen as *L. hilarianus* (US). Both specimens are similar and represent the taxon that we treat here as *Lupinus gibertianus* var. *reineckianus*.

Representative specimens. *An asterisk indicates a specimen included in this analysis. OTU numbers are in boldface and brackets. ARGENTINA. **Chaco:** Río Tragadero, 27 Sep. 1942, *Schulz 3530* (CTES*); Bermejo, Las Palmas, Oct. 1917, *Jørgensen 2139* (DS; SI* [1]); Primero de Mayo, Margarita Belén, 7 Nov. 1947, *Aguilar s.n.* (LIL 211346). **Corrientes:** Bella Vista, 5 Oct. 1976, *Fernández Velasco s.n.* (BA 68959); Capital, Parada Medina, 28 Sep. 1975, *Schinini & Martínez Crovetto 12213* (G); Escuela de Agricultura, 5 Oct. 1967, *Arbo 68* (BAA, CTES, MO); Prefectura, 30 Oct. 1966, *Krapovickas 1258* (CTES); Perichón, 29 Sep. 1974, *Krapovickas et al. 26450* (CTES* [4], LIL); General Paz, Puissoye, 26 Oct. 1945, *Ibarrola 3618* (LIL*); Itatí, 8 Oct. 1964, *Pedersen 7073* (B, LP, LSR, RNG, US); Ituzaingó, 30 Sep. 1993, *Planchuelo 618 B* (ACOR*); Ea. Santa Tecla, *Schwarz 8048* (LIL*); Mburucuyá, Ea. Santa Teresa, 8 Oct. 1954, *Cabrera 11642* (US); San Cosme, Paso de La Patria, 21 Feb. 1984, *Schinini & Martínez Crovetto 22785* (LIL*) [11], 25 Sep. 1988, *Krapovickas 42745* (BA*, G); road to Paso de La Patria, 29 Sep. 1993, *Planchuelo 611* (ACOR*) [13]; San Luis del Palmar, Route 5 and Riachuelo, 5 Oct. 1975, *Cristóbal 1331* (G); San Roque, Ea. Caaguazú road to Tacuaritas, 25 Oct. 1996, *Arbo et al. 6855* (LIL); Santo Tomé, Garruchos, 20 Sep. 1974, *Krapovickas 25780* (LIL*). **Entre Ríos:** Concordia, Sep. 1917, *Alazraqui s.n.* (BA 63399), 8 Nov. 1965, *Burkart 25960* (US*) [17]; camino al INTA, 4 Oct. 1993, *Planchuelo 656* (ACOR); Gualaguaychú, Paranacito, Nov. 1917, *Hauman s.n.* (BA 63397), Nov. 1931, *Daguerre s.n.* (BA 11965); Brazo Largo, 23 Oct. 1980, *Troncoso & Bacigalupo 2880* (US*) [20]; Médanos, *Parodi 9462* (BAA). **Misiones:** Campo Evé, 14 Jan. 1887, *Niederlein 1126* (BA*) [22]; Libertador General San Martín, Puerto Mineral, 24 Aug. 1950, *Schwarz 10685* (LIL*) [29]; San Ignacio, Oct., *Hassler 444* (G*) [30], 4 Feb.

1947, *Montes 878* (BA sheet A plant A); Menocchio, 12 Oct. 1945, *Schwarz 1256* (LIL); Santo Pipó, 3 Oct. 1947, *Schwarz 4874* (CTES, LIL), 23 Sep. 1948, *Schwarz 6143* (CTES, LIL); General Roca, 7 Oct. 1948, *Schwarz 6311* (LIL). **Santa Fe:** Capital, San José del Rincón, 5 Oct. 1911, *Álvarez 868* (LIL*); Colastiné, 8 Nov. 1946, *Álvarez 924* (LIL*) [43]; access to Túnel Subfluvial Hernandarias, 3 Nov. 1995, *Planchuelo 812* (ACOR*) [33]; Garay, Cayastá, 18 Oct. 1980, *Perrone s.n.* (BA 70851); General Obligado, Mocoví, 26 Oct. 1903, *Venturi 92* (BA, BAA* [37], CORD, DS, LIL, US); Las Colonias, Esperanza, 15 Nov. 1946, *Huidobro 3262* (LIL*). **Tucumán:** Chicligasta, 14 Oct. 1913, *Monetti 1245* (DS, LIL* [38]); Monteros, Río Monteros, 12 Oct., *Killip 39509* (US). BRAZIL. **Rio Grande Do Sul:** 1897, *Reineck & Czemark 93* (BA* [41], K). URUGUAY. **Colonia:** Artilleros, 17 Dec. 1943, *Bartlett 21221* (US*) [46].

2d. *Lupinus gibertianus* var. *berroanus* (C. P. Smith) Planchuelo & E. Fuentes, comb. et stat. nov. Basionym: *Lupinus berroanus* C. P. Smith, Spec. Lupinorum 14: 213. 1940. TYPE: Uruguay. Salto: 4 Nov. 1902, *Berro 2775* (holotype, K H 82/77–5; ACOR photo, UMO photo).

This variety is characterized by the leaflet size, 30–45 × 10–13(–15) mm with an LSC = 0.60–0.79, which represents the maximum expression of leaflet width independently of leaf and plant size. Free portion of the stipules 3–4 × 1.5 mm. Standard petal 8–10 × 7–9 mm.

Iconography. Figure 4D.

Representative specimens. *An asterisk indicates a specimen included in this analysis. OTU numbers are in boldface and brackets. ARGENTINA. **Chaco:** Primero de Marzo, Colonia Benitez, *Bacigalupo et al. s.n.* (BAA 9504*) [2]. **Corrientes:** Capital, Camino a Santa Ana, 29 Nov. 1993, *Planchuelo 609* (ACOR*) [5]; Concepción, Carámbola, 17 Dec. 1974, *Burkart et al. 30888* (US); Empedrado, 26 Sep. 1971, *Krapovickas et al. 19958* (CTES*); General Paz, 15 Oct. 1945, *Ibarrola 3523* (LIL*); Ituzaingó, 30 Sep. 1993, *Planchuelo 618 A* (ACOR*), 10 Oct. 1949, *Schwarz 8206* (LIL*); San Cosme, Paso de La Patria, 13 Oct. 1982, *Schinini & Martínez Crovetto 22785* (CTES*), 25 Sep. 1988, *Krapovickas 42745* (LIL*) [12]; Saladas, Laguna Soto Saladas, 26 Sep. 1944, *Schwarz 59* (LIL*). **Entre Ríos:** Concordia, 13 Nov. 1956, *Ruiz Leal 18349* (RL*) [16]; crossroads Rutas 14 y 22, 4 Oct. 1993, *Planchuelo 655* (ACOR*) [19]; INTA Concordia, 4 Oct. 1993, *Planchuelo 658* (ACOR*). **Misiones:** Apóstoles, 10 km of Azara, 31 Aug. 1974, *Arbo et al. 2300* (CTES*). **Santa Fé:** Capital, La Guardia, 19 Nov. 1946, *Huidobro 3069* (LIL); Guadalupe, 21 Nov. 1946, *Huidobro 3411* (LIL*); Castellanos, Rafaela, 15 Nov. 1946, *Huidobro 3423* (CTES*) [34]; Garay, Cayastá, 3 Nov. 1995, *Planchuelo 816* (ACOR*) [35]. **Tucumán:** Leales, Los Gómez, Río Salí, Nov. 1919, *Venturi 630* (DS, LP*); Monteros, Río Romero, 22 Nov. 1903, *Lillo 3281* (LIL*) [39]; Acherál, 500 msm, 11 Nov. 1923, *Venturi 2485* (BA, LIL* [40], US). URUGUAY. **Salto:** Salto, 4 Nov. 1902, *Berro 2775* (K*) [50]. **Colonia:** Colonia, 11 Nov. 1919, *Castellanos s.n.* (BA 56695*); Riachuelo, Oct. 1949, *Fabris 37* (LP*) [47].

Acknowledgments. The authors are indebted to the curators of the herbaria cited and to the botanists of the Smithsonian Institution and the Royal Botanic Gardens, Kew, for the kind attention received. Also special thanks are given to J. Michael Lock (K) for reviewing the manuscript and to Victoria C. Hollowell and Amy McPherson (MO) for their invaluable help during the editing of the paper. This research was partially funded by CONICOR, FONCYT, Fundación Antorchas, and SECYT of the Universidad Nacional de Córdoba, Argentina.

Literature Cited

- Crisci, J. V. & M. F. López Armengol. 1983. Introducción a la Teoría y Práctica de la Taxonomía Numérica. O.E.A., Washington, D.C.
- Dunn, D. B. 1984. Cytotaxonomy and distribution of New World lupin species. Proc. 3rd International Lupine Conference: 68–85. La Rochelle, France.
- & A. M. Planchuelo. 1981. *Lupinus heptaphyllus* (Velloso) vs. *Lupinus hilarianus* Benth. Taxon 30: 464–470.
- Fuentes, E. & A. M. Planchuelo. 1997. Sterol and fatty acid patterns in wild and cultivated species of *Lupinus* (Leguminosae). Z. Naturf. 52c: 9–14.
- & ———. 2000. Wild lupins as pioneers of riverside sand banks. Pp. 316–319 in E. van Santen, M. Wink, S. Weissmann & P. Roemer (editors), Lupin, an Ancient Crop for the New Millennium. Proc. 9th International Lupin Conference. Auburn University, Montgomery, Alabama.
- Merino, E. F., E. Fuentes & A. M. Planchuelo. 2000. Phytochemical characterisation of lupin species of South America. Pp. 291–293 in E. van Santen, M. Wink, S. Weissmann & P. Roemer (editors), Lupin, an Ancient Crop for the New Millennium. Proc. 9th International Lupin Conference. Auburn University, Montgomery, Alabama.
- , D. Maestri & A. M. Planchuelo. 1999. Chemotaxonomic evaluation of leaf alkanes in species of *Lupinus* (Leguminosae). Biochem. Syst. Ecol. 27: 297–301.
- Planchuelo, A. M. 1978. A Monograph of *Lupinus* for Argentina. Ph.D. Dissertation, University of Missouri–Columbia. Univ. Microfilm Inter. 39/10B, Order N1 7906915: 179.
- . 1982. Revisión bibliográfica del género *Lupinus*, Literature review of the genus *Lupinus*. Lupin Newslett. 4: 37–39.
- . 1994a. Wild lupin distribution and its implication as germplasm resources. Pp. 65–69 in J. M. Neves Martins & M. L. Beirao Da Costa (editors), Advances in Lupin Research. ISA-Press, Lisboa, Portugal.
- . 1994b. Quinolizidine alkaloid profiles of wild lupines from South America. The Science of Legumes (1): 81–85. Finland.
- . 1996a. Relationship between South American and European species of *Lupinus*. Pp. 109–116 in B. Pickersgill & J. M. Lock (editors), Advances in Legume Systematics 8: Legumes of Economic Importance. Royal Botanic Gardens, Kew.
- . 1996b. A new species of *Lupinus* (Fabaceae: Lupininae) from southeastern Brazil. Brittonia 48: 263–265.
- & D. B. Dunn. 1984. The simple leaved lupines and their relatives in Argentina. Ann. Missouri Bot. Gard. 71: 92–103.
- & ———. 1989. Two new species of the *Lupinus lanatus* complex. Ann. Missouri Bot. Gard. 76: 303–309.
- Planchuelo-Ravelo, A. M. 1984. Taxonomic studies of *Lupinus* in South America. Proc. 3rd International Lupine Conference: 40–53. La Rochelle, France.
- . 1991. Flower morphology of *Lupinus gibertianus* complex and its relation with cultivated species. Proc. VI International Lupin Conference: 366–372. Temuco-Pucón, Chile.
- , L. Witte & M. Wink. 1993. Quinolizidine alkaloid profiles of South American lupins: *Lupinus linearis* and the *Lupinus gibertianus* complex. Z. Naturf. 48c: 702–706.
- Rohlf, F. J. 1992. NTSYS-pc. Numerical Taxonomy and Multivariate Analysis System (vers. 1.70). Exeter Software, New York.